REVERSIBILITY OF THE REACTIONS OF PLANARIA DOROTOCEPHALA TO A CURRENT OF WATER.

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CONTENTS.

I. INTRODUCTION.

A reaction of planarians to currents of water has been described by Pearl ('03) in his careful study of the general features of the behavior of planarians. He has described the reaction and his method of obtaining it as follows: "In the course of the experiments to localize chemical stimuli by the capillary tube method, it was discovered that by means of a tube with a relatively large opening (from .25 to .50 mm. in diameter) and letting the ordinary tap-water in which the animals were flow out of it by its own weight, a current of just the right intensity to cause a positive reaction could be produced. The animals would turn very sharply toward the source of such a current, the reaction being evidently the same as that to other weak stimuli (chemical and mechanical). This reaction is localized in the same way as the usual positive reaction. It is given only when the current is directed against the head or anterior part of the body" (p. 698). He states that earlier in his work a large number of experiments were performed with various devices to determine whether these animals would show such a reaction, but without success. Streams of water from a

pipette and similar devices caused only a stopping, longitudinal contraction, and gripping of the bottom without any turning either toward or away from the source of the stimulus.

That the rheotropic reactions of planarians were found so difficult to demonstrate, it seems probable, must have been due to the experimental methods employed. Using the methods described below, it has been found that rheotropic reactions of these animals can be demonstrated very easily, not only in a "current of just the right intensity" but in currents of a large range of intensities. Under the conditions of these methods a worm is entirely surrounded by the flowing water on all surfaces except the ventral surface which is attached to the substratum, and the conditions of stimulation are more typically rheotropic than when the stream of water is directed as a small jet against a localized part of the body. A negative reaction, *i. e.*, a turning away from the side stimulated, was not described by Pearl but Dr. C. M. Child, who suggested this study, has observed a negative reaction as well as a positive reaction in currents of water in his laboratory stocks of worms used in studies in regeneration. It has been found that these reactions are reversible experimentally. The study of their reversibility which is reported in the present paper was preliminary to a more detailed study of the rheotropism of these animals which is in progress at the present time.

The work reported in the present paper was done some time ago in the zoölogical laboratory of the University of Chicago. My acknowledgments are due Dr. C. M. Child and Dr. V. E. Shelford for helpful suggestions.

II. Material and Methods.

Planaria dorotocephala has been used exclusively for this study. Specimens were collected from a spring-fed marsh at the margin of the Fox River near Chicago, Illinois. These animals are very easy to keep in the laboratory without special care. Since this study was in the nature of a testing of the reaction possibilities of the worms toward currents of water, rather than an effort to determine the normal habits, no efforts were made to duplicate the normal conditions of existence in

nature. Specimens were kept in large numbers in glass and galvanized iron containers which were emptied of water, rinsed and filled with fresh tap-water from time to time without removing the worms which cling to the surface of the vessel. They were fed two or three times a week with fresh beef cut into small bits and left in the dish for several hours or during the night. These worms collect on fresh meat and secure blood and juices but it is very improbable that they are able to make use of the solid portions.

Rheotropic reactions were tested in a "circular current" as follows: A considerable number of specimens, sometimes several hundred, were placed in a circular shaped vessel such as a glass battery jar or a kitchen pan and the water was stirred vigorously around the dish several times with a stirring rod. Vigorous stirring usually dislodged the most of the specimens which were then swept into a bunch at the center of the current. If they were not dislodged by the stirring, they were loosened by means of more vigorous streams of water from a large bulbed pipette. The movements of the animals on the bottom of the vessel only were studied since those on the sides were in a different relation to gravity which introduced a geotropic factor into the reaction. Rheotropism has been observed, however, in worms gliding on vertical surfaces.

It was found convenient to have all the specimens, or the larger part of them, enter the experiment at the center of the "circular current" since they were then all placed under similar conditions. In whatever direction any worm started out from the center, it would receive the current against the same side of the body as all the other worms starting from the center. If the current were stirred in the clockwise direction, for example, all the worms starting from the center of the dish would receive the current against the left side of the body. If they gave a positive reaction, they turned toward the left side; that is, toward the side stimulated, or up-stream, and if they gave a negative reaction, they turned toward the right side; that is, away from the side stimulated, or down-stream. When a large number of worms were gliding on the bottom of the dish, if their reactions were uniform, a very striking figure was produced.

This is illustrated in Figs. 1 and 2. Fig. 1 is a photograph of a lot of worms in a dish pan, reacting positively to a current stirred in the clockwise direction. The conspicuous spiral form of the figure is characteristic of the positive reaction. Fig. 2 is a photograph showing the characteristic negative reaction near the center of the pan.

These peculiar and characteristic spiral figures in a "circular current" called for a more careful examination of the physical conditions in the experiment, which revealed the fact that the worms were subjected to a system of spiral currents instead of a circular current. If a drop of a water suspension of carmine is placed on the bottom of a dish in which the water has been stirred in this way, the carmine in the lower layers of water close to the bottom will be seen to stream inward along a spiral course toward the center. Fig. 3 is a photograph of a dish pan in which the water was stirred in the clockwise direction and then drops of carmine were placed on the bottom at eleven points around its circumference. The carmine was dragged along by the currents and left streaks on the bottom of the pan which show as spiral lines in the photograph. The worms were subjected to this spiral system of currents. Carmine in the upper layers of water was swept about the dish in a fairly circular direction, and the water which flowed along the spiral lines on the bottom toward the center, rose, as it neared the center, and spread outward above.

A comparison of Fig. 3 with Fig. 1 shows that the spiral lines of the currents and the spiral lines of the positive reaction are alike. This explains, therefore, the spiral character of the reaction. The worms orient themselves to a spiral current. A comparison of Fig. 2 with Fig. 3 shows that in the usual negative reaction the direction taken is away from the side stimulated, but rather diagonally than directly down-stream. In some cases, however, when worms were distributed over the bottom and were not dislodged by the stirring, they were observed to turn inward and follow along the lines of the spiral current in as precise a negative orientation as was often characteristic of the positive reaction.

A mixture of definitely positive and definitely negative re-

actions at the same time, that is, an intermingling of the two systems of spirals, was not common. The reactions varied, however, in uniformity at different times; that is, in the precision of orientation, and in some cases the worms scattered from the center without forming any very definite spiral in either direction. Such "reactions" were designated "indefinite."

III. Difference of Reaction to Currents of Different Velocities.

In studying the reversal of rheotropic reactions induced by changing the chemical and thermal conditions, it was found that it is important to consider the velocity of the current. A change in the velocity of the current, or, in other words, in the strength of the rheotropic stimulus, may itself cause reversal of the sign of the reaction.

Since a current in a small vessel diminishes rapidly in velocity after the stirring is discontinued, the different worms in a single trial are subject to different velocities of current, the first worms to leave the center entering the strongest current and later worms finding successively weaker current. It was frequently observed that the positive reaction was given by the earlier worms; that is, those in the strongest current, and the negative reaction by the later worms; that is, those in the weaker currrent. The proportion of individuals giving each reaction varied in different observations while in some cases no negative reaction was given and in other cases no positive reaction was given.

A positive reaction in stronger current and a negative reaction in weaker current can be seen at the same time in a broad-bottomed pan where the negative spiral may begin about the center before the last individuals belonging to the positive spiral have reached the sides. This is possible because the current is swifter about the outside where the positive reaction is still being given than about the center where the negative reaction is beginning. Fig. 2 shows such a combination of positive spiral about the outside and negative spiral about the center. In the case which is photographed there is considerable irregularity in the positive spiral. In many cases the positive spiral about the outside was as regular as that in Fig. 1.

Table I. shows the total number of trials in which the different types of reaction were given during all the experiments.

Table I.

Summary of All Reactions Observed (Except Those Given upon Increasing the Velocity of the Current, for Which See Table II).

The sign + indicates a positive spiral, –, a negative spiral and ?, no dominant spiral of either sign. The sign + – indicates positive reaction in stronger current and negative reaction in weaker current; (+) – indicates only a few worms in the positive spiral, and + (–) only a few worms in the negative spiral.

Reactions.	Total Number of Trials of Worms in Normal Conditions Preceding Experiments, and in Normal "Controls" During Experiments.	Total Number of Trials During Experiments, in all Conditions, Excepting the "Controls."	Totals.
+	324	119	443
–	31	130	161
(+) –	45	48	93
+ –	46 } 113	36 } 104	82 } 217
+ (–)	22	20	42
?	32	29	61
Totals.....	500	382	882

In the observations described above, the same individuals were not observed to give both reactions because under the conditions of the tests the same individuals are not subjected to both extremes of current velocity. The earlier worms receive the stronger current and the later worms receive weaker current. It was readily shown, however, that the same individuals which responded negatively in a weaker current would respond positively in a stronger current. Upon second stirring of the water over a negative spiral without dislodging the worms, it was generally found that the worms composing the negative spiral reversed their direction of movement from negative to positive, so that the negative spiral became converted into a positive spiral composed of the same individuals. Out of 100 cases in which second stirring of the water over a negative spiral was tried, 80 cases showed reversal to positive. In some cases all the individuals gave this reversal while in other cases few individuals, that is, only those forming the outside of the spiral gave the reversal. In some cases reversal was readily induced by currents of moderate velocity while in other cases reversal was given only in very strong currents.

TABLE II.

REVERSAL OF REACTION INDUCED BY INCREASING THE VELOCITY OF THE CURRENT. SUMMARY OF ALL REACTIONS IN EXPERIMENTS IN WHICH THE VELOCITY OF THE CURRENT WAS INCREASED WHILE A REACTION WAS BEING GIVEN.

Velocity Increased During a Negative Reaction.

Complete Reaction Before Increase in Velocity.	Reactions After Increase in Velocity.				
	Reversal to +.	More Precise —.	No Change —.	Worms Dislodged.	Reaction Became ?.
—	21	5	5	1	1
(+) —	18	1	2		
+	28		3	2	
+ (—)	13				
Totals....	80	6	10	3	1

Velocity Increased During a Positive Reaction.

Complete Reaction Before Increase in Velocity.	Reactions After Increase in Velocity.		
	More Precise +.	No Change +.	
+	8	4	
? +	1		

Velocity Increased During an Indefinite Reaction.

Complete Reaction Before Increase in Velocity.	Reactions After Increase in Velocity.	
	Reaction Became +.	
?	4	
(+) ?	4	
+ ?	15	
+ (?)	1	

No evidence has been obtained that a stronger rheotropic stimulus will cause a negative reaction while a weaker stimulus causes a positive reaction. No observations showed a sequence of reactions during the diminution of the velocity of the current; of negative in stronger current and positive in weaker current (*cf.* Table I.). And second stirring of the current while the worms were distributed over the bottom was never observed to reverse the reaction from positive to negative. If the worms were giving the positive reaction in weaker current they continued to give the same reaction in stronger current, and usually with greater precision of orientation (Table II.). When the reaction was

"indefinite" in weaker current, the stronger current usually called forth the positive reaction.

IV. Reversal of Reaction Induced by Chemical Changes.

Reversal of reaction from positive to negative can usually be induced by pouring off the water from the worms and replacing it with fresh tap-water. Thus in 23 out of 24 observations this treatment resulted in reversal to the negative reaction. Two factors may be responsible for this reversal, change in temperature and change in the chemical composition of the water. Each of these factors was investigated by modifying the condition in question while preserving other conditions unmodified. The velocity of the current could not be preserved unmodified with the methods employed, but this factor was controlled indirectly.

The effect of changing the chemical character of the water was tested as follows: A lot of worms were tested in the water in which they were living at the time. Then an equal volume of fresh tap-water, or modified water, was brought to the same temperature as the aquarium water, and the worms were tested alternately in these two kinds of water.

A number of experiments were performed in which aquarium water was replaced by fresh tap-water of the same temperature. Since the rheotropic reaction in many cases may be positive in stronger current and negative in weaker current, it must be made certain that the reversal of reaction after a chemical change in the environment is a reversal of reaction in the same velocity of current. Although it seemed fairly certain to the operator, during the earlier experiments, that there was such a reversal in the same velocities of current, the later experiments were performed with a "control" to make them more conclusive. In these experiments two dishes of worms living under the same conditions, frequently in the same aquarium tank, were tested side by side. One lot of worms was tested in waters of different composition while the other lot was kept as the "control" and was tested always in the original aquarium water. The experimental and control dishes were placed side by side, and the control worms were tested at each trial simultaneously with

the experimental worms so that the conditions as regards velocity of current were practically the same in the two dishes. Progressive diminutions in velocity were practically the same in the two dishes. Differences of reaction given by the worms in the two dishes at the same time of observation must then be traced to other factors than the velocity of the current.

The following experiment will illustrate the method of the controlled experiments and the characteristic reversal of reaction induced by change from aquarium water to fresh water. Many hundreds of worms of miscellaneous sizes were tested in two large galvanized iron tanks. A current was produced by shaking

TABLE III.

EXPERIMENT SHOWING REVERSAL OF REACTION FROM POSITIVE TO NEGATIVE INDUCED BY CHANGE FROM AQUARIUM TO FRESH WATER AT THE SAME TEMPERATURE.

Trial.	Experiment.		Control.
	Water.	Reactions.	Reactions.
1	Aquarium	+ good general response	+ in strong current – in weak current
		+ on second stirring, even in weak current	+ on second stirring, universal.
2	Fresh	– even in fairly strong current.	+ even in very reduced current.
		– on second stirring, even in fairly strong current, a few + in strongest current	
3	Aquarium	– slight; worms slow in distributing on the bottom.	+ even in very weak current.
		+ on second stirring, even in only moderately strong current.	
4	Fresh	– even in fairly strong current.	+ even in very weak current.
		– on second stirring, no positive reaction.	
5	Aquarium	movement very slow, current reduced before any reaction was given.	+ even in very weak current.
		+ on second stirring only moderately strong current.	

the tanks in the hands, which swept the worms to the center. In the experimental tank aquarium water was used in trials 1, 3 and 5; and this was replaced by fresh water in the alternate

trials 2 and 4. In the control tank the worms remained in the aquarium water in all the trials. The temperature was 21° C. The reactions in each trial are described in Table III.

From the table it can be seen that placing the worms in fresh water reversed the reaction from positive to negative while returning them to their former aquarium water brought back the former positive reaction. These reactions were reversed back and forth by changing the water. The reversal of reaction cannot be attributed to a difference in the velocity of the current. The negative reactions in the fresh water were given in fairly strong current while the positive reactions in aquarium water were given in very weak as well as stronger current; and in the control, in which the velocity of the current was approximately the same at each moment as that in the experiment, a positive reaction was given at the same time that a negative reaction was observed in the experiment. In the two tests in this experiment with fresh water (trials 2 and 4), therefore, a change to fresh water induced a reversal of reaction from positive to negative while a return to the normal environment brought back the positive reaction. In 40 such tests in experiments at different times, a reversal from positive to negative was given in 21 tests and a reversal from negative to positive in 5 tests. In 7 tests a positive reaction remained unchanged while in 5 tests a negative reaction remained unchanged. In 2 tests the reaction was "indefinite."

Fresh water differs from aquarium water in oxygen content and in the absence of the metabolic products of the worms and the decomposition products that accumulate in the aquarium. The aquarium water in experiments at different times varied greatly in composition, while the fresh drawn tap-water probably varied little. It would seem that fresh water would make a more suitable environment than stale aquarium water where many worms have lived together without green vegetation. In the experiment described above the aquarium water was quite foul from the decomposition products of juices of meat that had stood in the aquarium for nearly 24 hours. When modified aquarium water was used instead of fresh water, reversal of the same sort was induced. In one experiment part of

the aquarium water was boiled, and in the two tests made with this boiled aquarium water reversal of reaction from positive to negative was obtained. In another experiment cane sugar was dissolved in part of the aquarium water to make a 1 per cent. solution which induced reversal from positive to negative in the 6 tests made. Similarly a well-mixed solution of juices of raw beef in aquarium water induced the same reversal in the 6 tests made. So far as these experiments indicate, therefore, the reversal of the rheotropic reaction in the new environment seems to be due more to the strangeness of the new conditions than to their fitness or unfitness. In a total of 54 tests with modified aquarium water and fresh water, reversal of reaction from positive to negative was induced in 35 tests, while in 5 tests the reaction was already negative from other causes. These figures may not necessarily represent the proportion of individual worm reactions which can be reversed in this way, since the conditions in different experiments were not entirely identical, but it may be repeated that in each of these tests a large number of worms were tested, in some cases many hundreds of individuals.

V. Reversal of Reaction Induced by Changes of Temperature.

The effect of changes of temperature upon the rheotropism was tested by dividing the water in which worms were living into two portions, preserving one portion at the temperature at which the worms were found at the beginning of the experiment, and cooling or warming the other portion to the desired temperature. The worms were then tested alternately in these two portions of water. It was found that the rheotropism can be reversed from positive to negative by lowering the temperature in the same manner as by changing the composition of the water.

In 34 individual tests, lowering the temperature by 4°–10° C. was found to cause a reversal in 17 tests from positive to negative, and reversal from negative to positive in 2 tests. In 4 tests this change in temperature made an indefinite reaction become positive. In the remaining 11 tests, lowering the temperature produced no observed change in reaction. This remained as before the temperature change; that is, as follows: positive in 7

tests, negative in 3 tests, positive in stronger current and negative in weaker current in one test.

The characteristic rheotropic effect, therefore, of lowering the temperature below that to which the worms are accustomed is a reversal of reaction from positive to negative. Return to the normal temperature brings back the positive reaction so that the reactions can be reversed back and forth by alternately lowering the temperature and raising it again to the normal. The reversal from negative to positive on raising the temperature seems to be due to the return to the temperature to which the the worms are accustomed, rather than to the fact that the temperature is raised, since in 13 tests of raising the temperature above the normal by 4°–10° C. reversal from negative to positive was obtained in only one case. In 4 tests the reversal was in the opposite direction; that is, from positive to negative. In 5 tests the negative reaction remained unchanged and in 2 tests the positive reaction remained unchanged, while in one test the reaction became "indefinite."

VI. Variations in Rheotropic Reactions.

The general features of the rheotropic reactions of planarians and their reversibility described above were observed in mass tests of large numbers of individuals. These depend upon considerable uniformity in the behavior of the different individuals in the trial, much as do the behavior experiments with cultures of protozoa. The uniformity of the reactions of the different individuals in a single trial in the experiments with planarians was generally very striking, at least with respect to the sign of the reaction in the same velocity of current. The precision of the reactions of different individuals varied greatly in different trials, although the sign of the reaction was definite. When the reaction is definitely either positive or negative, the characteristic spiral figure is very striking, and when a spiral could not be seen, the reaction was called indefinite. Only a small number of trials, however, failed to show a general uniformity in the sign of the reaction in the same velocity of current (Table I.).

The different tests of reversal in the same experiment generally gave fairly consistent results although with some variations

among the different tests. But in some experiments the lot of worms gave consistent results directly opposite to those generally obtained. Thus in the experiments of lowering the temperature, five of the seven tests in which the positive reaction remained unchanged were the successive tests in a single experiment. In this case the temperature at the beginning of the experiment, and the amount of the depression of the temperature, were the same as in other experiments in which reversal of reaction was produced in the characteristic manner. Such differences in behavior must be attributed to that complex of internal processes which has been characterized the "physiological state" of the organism.

VII. Reactions to Currents of Water in Nature.

That rheotropic reactions are normal to the life of planarians in nature is shown by field observations. The specimens studied in the laboratory were collected in a spring-fed marsh at the edge of the Fox River near Chicago, called "Station 10 Cary Spring" in Shelford's description of the animal communities of the Chicago Region (Shelford, '13, pages 52, 93 and 118). The marsh bottom is composed of black humus without stones under which the worms could collect in the manner that Pearl found characteristic of this species in the Huron River, but an abundance of leaves serves the same purpose. The water is very shallow and well shaded by marsh vegetation. There is a sluggish current fed by springs at the upper edge of the marsh, where water cress is found growing.

A small channel about five inches wide and fifteen feet long was discovered at the edge of the marsh through which a moderate current of water was flowing. A large number of worms were found in this stream, some moving on the bottom, generally up-stream, but most of them at rest on the under sides of leaves or in sheltered places on the bottom. Removing the shading vegetation for better observation stimulated many of the worms at rest to become active, and half an hour later 60 worms were counted going up-stream and 5 going down-stream and 200 were counted at rest on the under side of leaves. At that time the sun was shining somewhat from the side, and down-stream, but

it was not far from vertical as it was 11:30 in the morning. At 12:20 only 4 worms could be found in sight, 3 going up-stream and one going down-stream. At 1:30, when it was cloudy, 40 worms were found going up-stream and 4 going down-stream. At 3:10 a piece of raw beef was placed in the upper part of the stream and fifteen minutes later 176 worms were counted going up-stream and 34 going down-stream. It has frequently been noted that worms in a moderate stream of water will respond in this way and collect upon a piece of fresh beef and this behavior has been put to practical advantage in collecting specimens. Worms removed from this stream and tested in a circular pan by the method employed in the laboratory showed both the positive and the negative reactions very clearly, the positive in stronger current and the negative in weaker current, as described above.

These observations show that planarians may react to currents of water in nature. Pearl considered it "very improbable that this reaction is of any importance in the normal activity of the animal." This opinion may have been due to the difficulty which he experienced in demonstrating the reaction experimentally which might lead one to think that unusual conditions are necessary for its production in nature; whereas it has been shown that the reaction is given with readiness under experimental conditions which are similar to those in a natural stream of water, and also that it can be observed in nature. It would seem that a reaction which is so characteristic of the animals in the laboratory would play a part in their daily life in nature, when they live in an environment which offers the appropriate stimuli for the reaction. These animals seem to belong characteristically to stream communities where these conditions are fulfilled.

VIII. Summary.

1. *Planaria dorotocephala* show both positive and negative reactions in a stream of water.

2. The sign of the reaction may differ, depending upon the velocity of the current. The positive reaction is then given in stronger current and the negative reaction in weaker current.

3. A negative reaction in weaker current can often be reversed to the positive by increasing the velocity of the current.

4. Reversal of reaction from positive to negative can be induced by changing the composition of the water; and from negative to positive by return to the former conditions.

5. Similar reversals of reaction can be induced by sudden changes in temperature.

6. Rheotropic reactions are given by *Planaria dorotocephala* in nature.

7. Rheotropic reactions are very characteristic of these animals in the laboratory, rather than unusual as has been supposed.

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EXPLANATION OF PLATES.

PLATE I.

FIG. 1. The positive spiral. Photograph of worms giving a positive reaction to a current of water stirred in the clockwise direction.

FIG. 2. The negative spiral. Photograph of worms giving a negative reaction to a current of water stirred in the clockwise direction. The worms near the center are reacting negatively while those about the outer part of the pan, in the stronger current, are reacting positively.

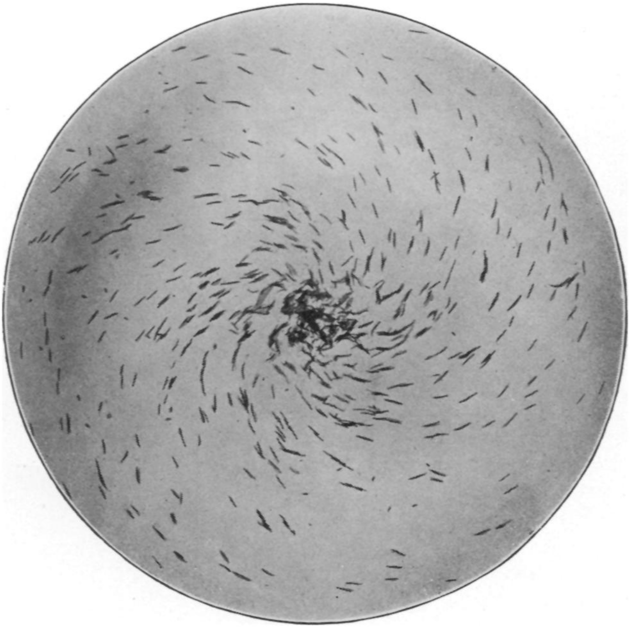

FIG. 1.

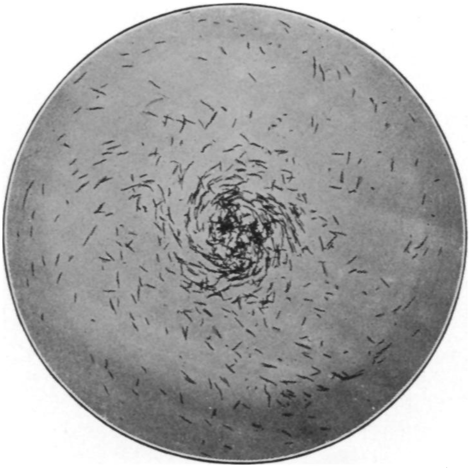

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FIG. 2.

PLATE II.

FIG. 3. The system of spiral currents. Photograph of pan in which the water has been stirred in the clockwise direction and then drops of carmine have been placed on the bottom at various points about its circumference. The dark lines are streaks of carmine produced by the currents and showing the direction of the currents upon the bottom.

FIG. 4. A positive reaction showing individual variation in the precision of orientation.

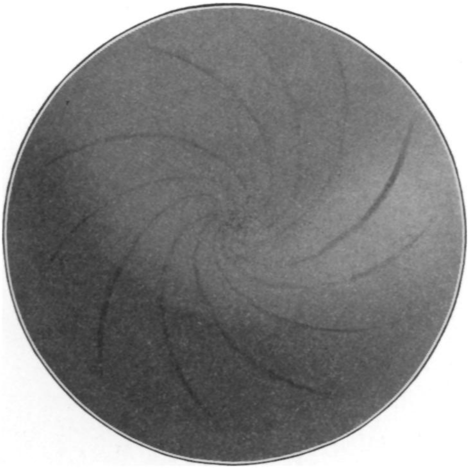

FIG. 3.

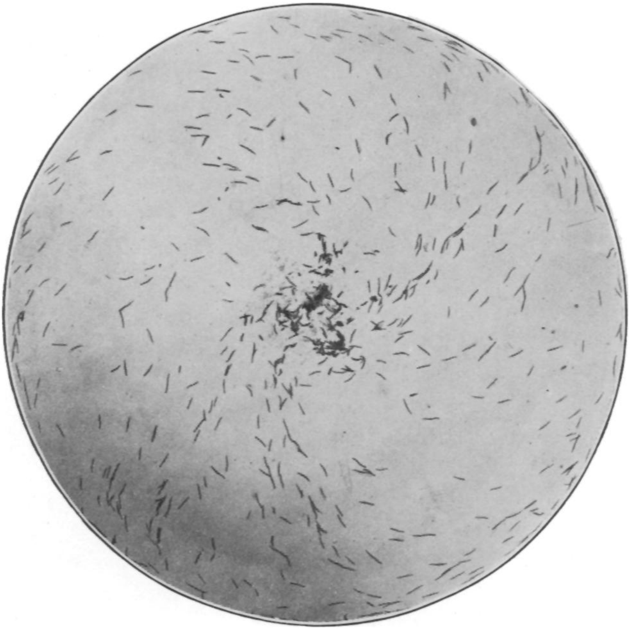

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FIG. 4.